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Long-Term Abundance Patterns of *Hexagenia* (Ephemeroptera: Ephemeridae) in Southern Indian Lake, Manitoba: Responses to Weather and Hydroelectric Development

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LONG-TERM ABUNDANCE PATTERNS OF *HEXAGENIA* (EPHEMEROPTERA: EPHEMERIDAE) IN SOUTHERN INDIAN LAKE, MANITOBA: RESPONSES TO WEATHER AND HYDROELECTRIC DEVELOPMENT

by

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TABLE OF CONTENTS

	Page
ABSTRACT/RÉSUMÉ	iv
INTRODUCTION	1
MATERIALS AND METHODS	1
Correlations between air temperature and *Hexagenia* abundance	2
RESULTS	3
DISCUSSION	3
Lakewide abundances	3
Regional abundances	3
Region 6E	4
Region 6W	4
Regions 5 and 7	4
Regions 3 and 4	4
CONCLUSIONS	5
ACKNOWLEDGMENTS	5
REFERENCES	5

LIST OF TABLES

Table		Page
1	Correlation analyses between whole-lake *Hexagenia* abundance and air temperatures in Southern Indian Lake, 1972-1987. (See text for explanation; dd = degree days)	7
2	Average dates of break-up and freeze-up, length of ice-free season, and mean summer temperatures (°C) for Southern Indian Lake, 1972-1987	8
3	Correlation analyses between air temperature accumulations [degree days (dd) >0°C, open-water season] and water temperature accumulations (dd>8°C) for regions 1, 2, 4, 5, and 6, Southern Indian Lake, 1972-1979	9

LIST OF FIGURES

Figure		Page
1	Natural and diversion flows of the Churchill River in northern Manitoba (latitude in °N, longitude in °W)	10
2	Summary of the 3-yr *Hexagenia* life cycle and the factors influencing abundance of *Hexagenia* in Southern Indian Lake (from Giberson 1991)	11
3	Southern Indian Lake (SIL), showing regions (numbers), whole-lake survey sampling sites (dots), and location of the SIL camp and weather station. Arrows refer to major inflow and outlets	12
4	Annual air temperature accumulations >0°C (1969-1987) and whole-lake *Hexagenia* abundance (no.m^{-2}, 1972-1987), for Southern Indian Lake (dd = degree days)	13
5	Relationship between *Hexagenia* whole-lake abundance (mean no.m^{-2}) and 3-yr accumulated air temperatures (>0°C) in Southern Indian Lake, 1972-1987	13
6	Relationship between mean summer temperature (°C) and number of windy days during July and August for Southern Indian Lake, 1978-1989	14
7	Comparison between observed *Hexagenia* abundances and those predicted from the relationship shown in Fig. 5	14
8	Relationships between *Hexagenia* abundance and 3-yr accumulated air temperatures for the nine regions in Southern Indian Lake, 1972-1987. Asterisks refer to the level of statistical significance: *$p<0.05$; **$p<0.01$; ***$p<0.001$	15
9	Comparison between observed *Hexagenia* abundances (dashed line) and those predicted (solid line) from the relationships in Fig. 8	16

ABSTRACT

Giberson, D.J., D.M. Rosenberg, and A.P. Wiens. 1992. Long-term abundance patterns of Hexagenia (Ephemeroptera: Ephemeridae) in Southern Indian Lake, Manitoba: responses to weather and hydroelectric development. Can. Tech. Rep. Fish. Aquat. Sci. 1837: iv + 16 p.

In the mid 1970s, Manitoba Hydro impounded Southern Indian Lake (SIL) and diverted much of the flow of the Churchill River, which flowed through SIL, into the Nelson River catchment for hydroelectric power generation. A dramatic decline in burrowing mayfly (Hexagenia) populations following lake manipulation was originally attributed to the physical effects of impoundment and diversion. Further monitoring, however, showed a recovery of the population, despite the ongoing physical impacts, so other factors were investigated in an attempt to explain the post-impoundment decline in Hexagenia abundance. Between 1972 and 1987, whole-lake Hexagenia abundances (no. m^{-2}) were strongly correlated to air temperatures during the summer (ice-free) periods (r^2 = 0.95), suggesting that weather, rather than hydroelectric development, was controlling population abundance. Summer air temperatures, in turn, were significantly correlated to water temperatures during Hexagenia development and weather during emergence, both of which are known to affect Hexagenia abundance. Impoundment of SIL and water diversion through it also influenced water temperatures, particularly in the lake regions most affected by Churchill River diversion. Because the magnitude of those effects varied with hydrogeographic region within the lake, it was possible to examine the relative importance of weather and hydroelectric development on Hexagenia abundance in different parts of the lake. Patterns of population abundance in five of the lake regions were apparently due mainly to weather, whereas those in the remaining four regions resulted from impoundment and/or diversion effects as well as weather. However, abundances in the latter four regions traditionally made up only a small portion of lake-wide abundance, so the impact of hydroelectric development was masked by the much larger natural, weather-related response.

Key words: burrowing mayflies; Churchill-Nelson diversion; lake impoundment; air temperatures; degree days.

RÉSUMÉ

Giberson, D.J., D.M. Rosenberg, and A.P. Wiens. 1992. Long-term abundance patterns of Hexagenia (Ephemeroptera: Ephemeridae) in Southern Indian Lake, Manitoba: responses to weather and hydroelectric development. Can. Tech. Rep. Fish. Aquat. Sci. 1837: iv + 16 p.

Vers le milieu des années 70, la compagnie Manitoba Hydro a endigué le lac Southern Indian et détourné une grande partie du débit de la rivière Churchill à travers le lac Southern Indian (SI), vers le bassin de la rivière Nelson, pour produire de l'hydroélectricité. On a initialement imputé un déclin dramatique des populations d'éphémères à larve fouisseuse (Hexagenia) survenu après la manipulation du lac, aux effets physiques de la retenue et du détournement des eaux. Toutefois des observations plus poussées ont indiqué un rétablissement des populations, malgré les incidences physiques continues, et l'on a donc étudié d'autres facteurs pour tenter d'expliquer le déclin de l'abondance de Hexagenia après l'endiguement. Entre 1972 et 1987, on a observé une étroite corrélation entre l'abondance de Hexagenia à l'échelle du lac tout entier (no. m^{-2}) et les températures atmosphériques au cours de l'été (périodes libres de glaces) (r^2 = 0.95), de qui suggère que le temps, et non l'aménagement hydroélectrique, régit l'abondance des populations. On a également établi une corrélation significative entre les températures atmosphériques estivales et la température de l'eau durant le développement de Hexagenia, et les conditions météorologiques au moment de l'émergence de l'insecte, ces deux dernières conditions ayant une influence reconnue sur l'abondance de Hexagenia. L'endiguement du lac SI et la diversion des eaux à travers ce lac ont également influencé la température des eaux, en particulier dans les régions des lacs les plus touchées par le détournement de la rivière Churchill. Comme l'ordre de grandeur de ces effets variait en fonction de la région hydrogéographique dans les limites du lac, il nous a été possible d'examiner l'importance relative des phénomènes météorologiques et des aménagements hydroélectriques sur l'abondance de Hexagenia dans diverses parties du lac. Les schémas d'abondance des populations dans cinq des régions du lac étaient apparemment surtout le résultat des phénomènes météorologiques, tandis que les schémas observés dans les quatre régions restantes étaient le résultat de la retenue ou de la diversion des eaux, ou des deux, autant que des conditions météorologiques. Cependant, l'abondance dans les quatre dernières régions ne représente habituellement qu'une faible proportion de l'abondance à l'échelle du lac tout entier, de sorte que l'incidence de l'aménagement hydroélectrique a été masquée par une réponse naturelle beaucoup plus prononcée, associée aux phénomènes météorologiques.

Mots-clés: éphémères à larve fouisseuse; détournement ou dérivation des rivières Churchill-Nelson; endiguement du lac; température atmosphérique; degrés-jours.

INTRODUCTION

A basic problem in monitoring industrial developments is discriminating between natural ecosystem variability and anthropogenic effects. Although good examples of the possible confusion of these factors exist for marine habitats (Bowman 1978; Cullinane and Whelan 1983), few are available for fresh waters. Between 1972 and 1987, results from benthic surveys of Southern Indian Lake (SIL), northern Manitoba, provided an example of how the causes of dramatic changes in standing stocks of biota can be misinterpreted.

SIL, a large lake on the Churchill River, is part of a major hydroelectric development in northern Manitoba. Manitoba Hydro's long-term plan to develop the 10,000-MW hydroelectric potential of the nearby lower Nelson River called for diversion of a licensed maximum of approximately 850 m^3 sec^{-1} of water (approximately 75% of total flow) from the Churchill River into the Nelson catchment at SIL (Newbury et al. 1984). The Churchill flows into SIL from the southwest and, prior to diversion, exited from the northeast on its way to Hudson Bay (Fig. 1). In 1976, the natural outlet of SIL was dammed and water levels in the lake rose 3 m above the long-term average. By fall 1977, the diversion was operating at full capacity through a newly excavated channel leading from the southeastern part of the lake into the Nelson catchment.

Abundances of the benthic macroinvertebrate community as a whole responded to impoundment by initially increasing, remaining high for a few years, and then decreasing to near pre-impoundment levels (Giberson et al. 1991). A post-impoundment "trophic upsurge", typical of new reservoirs, results from an initial input and then subsequent depletion of nutrients and organic matter originating from newly flooded land (Wiens and Rosenberg 1984). In SIL, it was estimated that 200,000 t of carbon, 2490 t of nitrogen, and 295 t of phosphorus were initially added to the lake from breakdown of black spruce needles alone (Crawford and Rosenberg 1984).

However, one major group of benthic macroinvertebrates, the burrowing mayflies (Hexagenia), did not increase in abundance in response to increased food supply in the lake. A slight increase in whole-lake abundances was observed immediately following impoundment (1977), but then population numbers declined sharply until, by 1981, Hexagenia appeared to have been virtually eliminated from the lake (Giberson et al. 1991). The reduction in Hexagenia standing stocks was initially attributed to: (1) an inability of Hexagenia to maintain their burrows in the sediment because of severe shoreline erosion and altered substrate composition; and (2) a decrease in water temperature in the northern part of the lake because of river diversion (Rosenberg and Wiens 1985). However, continued sampling of the lake (1983-1987) indicated a partial recovery of the population, despite continued shoreline erosion and altered thermal patterns, suggesting that other factors may have influenced Hexagenia abundance.

An intensive study to evaluate the importance of various physical factors in controlling Hexagenia abundance in SIL showed that life-history responses to weather variables had an important influence on population abundance (Giberson 1991; Fig. 2). Adult body size and fecundity, egg hatching success and timing, and duration of the life cycle (and, therefore, potential accumulated mortality) were dependent on water temperature during development (Giberson 1991). Because the lake usually did not stratify thermally, water temperatures were related to weather (as measured by air temperatures) during the open-water period (Hecky 1984). Air temperature during the adult emergence period influenced duration of the winged stages, potential exposure to predators, and mating success (Giberson 1991). Finally, wind conditions during emergence affected emergence, mating, oviposition success, and recruitment of the next generation (Giberson 1991).

In addition to weather effects, water temperatures were influenced by the impoundment of SIL and the diversion of the Churchill River into the Nelson catchment (Hecky 1984). Impoundment affected water temperatures throughout the lake by increasing the water volume to be heated, and by increasing light reflectance because of higher turbidity caused by eroding shorelines. Impoundment effects, however, were not as pronounced as those due to diversion. Diversion resulted in the redirection of most of the Churchill River southward, which delayed spring ice break-up in the large northern basins (regions 3 and 4 and the northern portion of region 2; Fig. 3), and resulted in cooler overall water temperatures (Hecky 1984). In addition, cooler Churchill River water moving out of region 2 into region 6W caused a cooling in region 6W (Hecky 1984). Therefore, the potential existed for temperature-related population effects caused by hydroelectric development to be superimposed on population effects caused by natural fluctuations of weather. The objective of this study was to determine the relative importance of weather and aspects of hydroelectric development to Hexagenia populations in SIL.

MATERIALS AND METHODS

Hexagenia were sampled in 1972 (before impoundment and diversion), 1977 (after impoundment but before full diversion), 1979 (after diversion), and every two years thereafter until 1987. Samples were collected during mid-July with a 15 X 15 cm weighted Ekman grab, along

with physical data (temperature, turbidity, sediment particle size distribution), at 58 stations throughout the lake (Fig. 3; Wiens and Rosenberg 1984; Giberson et al. 1991). Replicate samples were collected from each station in 1972 and three samples were collected from each station in subsequent years. Station abundances (no. m^{-2}) were averaged for each region or for the whole lake to yield regional and whole-lake abundances.

Data on local air temperature, precipitation, and wind speeds and directions were available from an Environment Canada weather station on SIL (Fig. 3) from 1978-1989. Weather data prior to 1978 were available from Lynn Lake (130 km west) and Thompson (130 km southeast); air temperatures for SIL for that period were estimated by taking the mean of the temperatures from those two weather stations (McCullough 1981).

Water temperatures were measured directly at a central location in regions 1, 2, 4, 5, and 6 during 1972-1979 (Hecky 1984). The relationship between air temperatures [degree days (dd) >0°C] and water temperatures (dd>8°C) was determined by regression and used to extend the period of record for water temperatures.

Hexagenia emerged at SIL mainly during July and August, so an analysis of wind magnitudes and durations was restricted to that period. Anecdotal information suggested that warm summers tended to be relatively calm, whereas cool summers were stormier and windier, so the relationship between mean summer temperature and number of windy days in July and August was determined by regression. A day was considered to be "windy" if wind speeds exceeded 15 km h^{-1} for at least two consecutive hours during the day.

Air temperature was chosen as the primary weather variable in correlation analyses with Hexagenia abundance because of its effect on life history and because of the relatively complete air temperature record that existed for the area. Although water temperature affects many aspects of the life history of Hexagenia, water temperature data were not continuous through the study period because of changes in the focus of research at SIL. In addition, water temperatures were not recorded for many of the locations where Hexagenia was found. For certain regions, water temperature accumulations could be estimated for missing years from previously established relationships between air and water temperatures, but such relationships were not available for some study locations. Therefore, it was simpler and more direct to use air temperatures alone, particularly since air temperature, water temperature, and wind condition are closely related.

Hexagenia growth and development are influenced by both the temperature during the growing season and the duration of the growing season. Therefore, daily temperatures were summed over the length of the ice-free season to give air dd>0°C. Air dd>0°C are roughly equivalent to the mean summer temperature multiplied by the number of ice-free days, and provide a relative measure of the amount of heat available each year for growth. Air dd>0°C were calculated for the entire open-water period, rather than just the period when water temperatures were above the developmental threshold temperature for Hexagenia (~8°C; Giberson 1991, chapter III), because any air temperatures above freezing in the spring influence the rate of warming and the start of growth. Similarly, in fall, rates of cooling may have an effect on life-history features such as egg hatch, and adults may still be emerging despite the cool temperatures (Giberson 1991, chapter III).

SIL ice-free periods for 1972-1979 are provided by McCullough (1981), and were calculated for 1980-1987 according to the formula in McCullough (1981). Date of average break-up for SIL was calculated as the intersection of the 40-day running mean temperature with 5°C, and freeze-up corresponded to the intersection in fall with 0°C; these dates corresponded well to the observed dates of break-up and freeze-up reported in McCullough (1981).

CORRELATIONS BETWEEN AIR TEMPERATURE AND HEXAGENIA ABUNDANCE

Hexagenia abundance (no. m^{-2}) and accumulated air temperatures (dd>0°C) were plotted against year for the period 1972-1987 (Fig. 4). Visual analysis of the plot suggested that Hexagenia abundance followed the temperature data, with a time lag of 2-3 yr. Consequently, a series of "lagged" regressions were examined to determine the relationship that explained (statistically) the most variation in Hexagenia abundance.

Two series of regressions were done:

(1) Single-year temperature accumulations - Hexagenia abundance was regressed against temperature accumulations (dd>0°C) for the previous summer open-water period, the summer 2 yr prior to the sampling date, and 3 yr prior to the sampling date.

(2) Multiple-year average accumulations - This series was based on the fact that temperature has an important influence on Hexagenia abundance over its entire life cycle. Hexagenia density was regressed against temperature accumulations for the entire annual open-water period (i.e. July-July, and including the period immediately prior to emergence) for 1 yr prior to the sampling date, and against the mean annual accumulated temperatures for 2 yr and 3 yr prior to the sampling date.

The strongest correlation was observed between Hexagenia abundance and the 3-yr accumulated air temperature (Table 1; Fig. 5). The relationship explained, in a statistical sense, nearly 95% of the variation in abundance between 1972 and 1987. The resulting regression equation:

$$Y = 0.152 (X) - 235$$

where: Y = abundance and X = dd>0°C

was used to predict lakewide Hexagenia abundance values for that period, based solely on the temperature relationship. Predicted abundances were plotted along with the observed values and compared visually. Hexagenia mean abundance was also calculated annually for each lake region and regressed against the 3-yr mean accumulated temperature. It was assumed that regions whose abundances did not significantly correlate to the air-temperature model were affected by factors in addition to weather.

RESULTS

Mean summer air temperatures for the SIL region varied from 10.8-13.8°C, and the length of the ice-free season ranged from 120-190 d between 1972 and 1987 (Table 2). Air dd>0°C ranged from 1344-2125/summer in that period ($\bar{x}$ = 1810) and showed high year-to-year variability (Fig. 4). Hexagenia abundance was high in 1972 and 1977, following periods of generally above average temperature accumulations, but dropped dramatically following the extremely cold years of 1978 and 1979 (Fig. 4). Temperature accumulations since 1980 have hovered near the 19-yr mean, and abundances of Hexagenia appear to be gradually recovering.

Accumulated air temperatures (dd>0°C, open-water period) were significantly correlated ($p<0.05$) to accumulated water temperatures for each region for which temperature data were available (Table 3). There was also a significant ($p=0.004$) trend for cool summers to be windier than warm ones (Fig. 6).

Predicted vs observed abundances of Hexagenia in SIL, based on the previously derived abundance/air temperature relationship, are shown in Fig. 7. Close agreement can be seen between the two, except for the early 5-yr gap in the sampling record.

Hexagenia abundance also showed a good relationship with air temperature on a regional basis in SIL, although the relationships for each region differed (Fig. 8). Correlations were significant ($p<0.05$) in all except regions 3 and 4, although correlations were weak in regions 5 and 7. Note, however, that in region 6E, a relatively strong correlation ($r^2=0.64$, $p=0.03$; Fig. 8) resulted from two clusters of points rather than a smooth linear distribution.

When relationships obtained from Fig. 8 were used to predict regional abundances on the basis of air temperature, the following patterns emerged (Fig. 9): (1) Observed abundances in regions 0, 1, 2, and 6W agreed closely with the temperature model, as expected from the high correlation coefficients (Fig. 8). (2) Regions 5 and 7 had generally higher than predicted mean Hexagenia abundances for the first half of the study period, and lower than those predicted for the second half. (3) Region 6E had higher abundances than predicted early in the study period, and abundances declined earlier than predicted, although they did not reach the very low levels expected from the temperature model; subsequently, abundance in 6E did not recover to the level predicted by the model. (4) Regions 3 and 4 showed similar patterns to region 6E, except that abundances did reach the very low levels (ca 1980) predicted by the model.

DISCUSSION

LAKEWIDE ABUNDANCES

High correlations between accumulated air temperatures and Hexagenia abundance in SIL stem from weather effects on the life history (Fig. 2; Giberson 1991). Air temperature during the ice-free season was directly related to water temperature because the lake does not stratify (Hecky 1984), and water temperature influenced life-cycle duration, egg-hatching success, emergence timing, and body size and fecundity (Giberson 1991, chapter III; Giberson and Rosenberg 1992a, b). Air temperature also affected the length of the subimaginal (winged sub-adult) stage, and consequently the length of time that Hexagenia was susceptible to predation in the winged stages (Giberson 1991, chapter III). Finally, cool summers tended to be relatively windy compared to warm summers and windy conditions hindered emergence and mating, so air temperature was also related indirectly to emergence success (Giberson 1991, chapter III). These temperature effects occur throughout the life cycle, so it is not surprising that the multiple-year temperature correlations produced statistically significant ($p<0.05$) results. The majority of the burrowing mayflies in SIL have a 3-yr life cycle (Giberson 1991, chapter III), which explains the good fit between Hexagenia abundance and 3-yr temperature accumulations.

REGIONAL ABUNDANCES

The temperature model was less useful when mean abundances were considered regionally rather than for the whole lake, despite significant ($p<0.05$) correlations between temperature and

abundance in all regions except 3 and 4. Regional differences in the relationship between Hexagenia abundance and temperature (Fig. 8) were caused by regional differences in physical characteristics such as depth and flow rate. Good correlations were expected in regions essentially unaffected by diversion (0,1, and most of 2), and those expectations were confirmed.

Region 6E

Region 6E had a significant correlation only because the data points for the period before and after lake manipulation fell into two clumps at either end of the regression line; this indicated an effect caused by factor(s) other than temperature.

Region 6E was unaffected by diversion, so Hexagenia abundance was expected to correlate well with weather patterns. However, numbers fell earlier than predicted from the weather model, did not reach the lowest values predicted by the model, and did not rebound to the same extent as other unaffected regions in the last years of the study. Abundances never reached the lowest values predicted perhaps because impoundment in this shallow region involved extensive amounts of shoreline, thereby producing increased food resources that offset temperature effects. Failure of Hexagenia abundances to rebound in the last years of the study may have been caused by low dissolved oxygen concentration during this period. Grab samples taken in region 6E during the last years of the study were highly organic and had a strong hydrogen sulfide smell, particularly in mid-summer. The addition of organic matter from shoreline erosion (caused by impoundment) to this area of shallow, sheltered bays together with a return to warmer temperatures may have produced a high oxygen demand, resulting in anoxic conditions that directly affected Hexagenia. Hexagenia cannot survive oxygen concentrations less than approximately 1.2 ppm (Hunt 1953; Eriksen 1968), so their low densities in this region could be related to low oxygen levels.

Region 6W

The strong correlation between air temperatures and Hexagenia abundances in region 6W was unexpected, because inputs of cool Churchill River water resulted in cooler summer water temperatures there than before diversion. However, Churchill River inputs opened up the area sooner in spring than in the pre-diversion condition, which probably resulted in a longer growing season and total temperature accumulations similar to the period before diversion (Hecky 1984). In addition, river flow may have increased organic inputs to the region. Food supply affects growth and development of Hexagenia, although to a lesser degree than temperature (Giberson and Rosenberg 1992a); an abundance of food may have compensated for lower water temperatures.

It is also possible that water temperature declines due to the diversion may have changed the life-cycle pattern in region 6W. Information on pre-diversion life-cycle patterns and temperature accumulations in 6W is not available, but if pre-diversion temperatures in 6W were similar to those in 6E, a 3-yr life cycle would have been expected. Nymphs in region 6W now require 4 yr to complete development (Giberson 1991, chapter III), so diversion may have also resulted in a lengthening of the life cycle. If the life cycle did change as a result of diversion effects on temperature, expected declines in abundance from a lowered temperature regime may have been offset by higher fecundity. Body length in Hexagenia (particularly H. limbata) was directly related to fecundity, and mean body length associated with the 4-yr life cycle in region 6W was considerably greater than that observed for the 3-yr life cycle in region 6E (Giberson 1991, chapter III).

Regions 5 and 7

Abundances in regions 5 and 7 showed significant correlations with air temperature, but correlations were relatively weak when compared to regions directly in the flow of the Churchill River. Neither region should have been affected by the diversion, and so both were expected to conform well to the weather model. In region 5, the weaker correlation could stem from the fact that it is located nearly 100 km north of the weather station, and weather patterns may have been different for the far northern portion of the lake. Region 7 was not sampled regularly, so little is known about physical conditions there and it is difficult to speculate on the reasons for the poor correlation. However, region 7 is deep and many parts are relatively sheltered, so impoundment may have resulted in occasional stratification and oxygen deficits. The sensitivity of Hexagenia to low oxygen concentrations has been discussed above.

Regions 3 and 4

Regions 3 and 4 were directly affected by diversion of the Churchill River southward, so the decline in abundances in these areas was probably related to a combination of weather and diversion effects. The decline in regions 3 and 4 was first noted in 1979, before areas primarily affected by weather, suggesting that diversion had an immediate effect. The combination of two consecutive cold years and lowered water temperatures because of diversion essentially eliminated Hexagenia from these regions. Abundances here originally were lower than in most other parts of the lake, so the patterns identified in regions 3 and 4 would have had little effect on whole-lake abundances.

CONCLUSIONS

The dramatic decline in Hexagenia populations in SIL following lake manipulation for hydroelectric development was largely a weather-related phenomenon rather than one caused by the manipulation. Ninety-five percent of the variation in lakewide abundances could be statistically explained by one weather variable - air temperature - which was related to both water temperatures during Hexagenia development and weather conditions during emergence. Intensive study of Hexagenia indicated some of the mechanisms for population control by weather, and suggested that water temperature was an important controlling variable. Because lake manipulation also influenced water temperatures in certain regions of the lake, a further analysis identified possible localized manipulation effects within specific regions. Hexagenia abundance in regions 0, 1, 2, 5, 6E, 6W, and 7 were significantly correlated with air temperature, whereas abundance patterns in regions 3 and 4 were not. In region 6E, despite an apparent correlation between abundance and weather, the pattern of Hexagenia abundance was most likely related to the effects of impoundment: Hexagenia abundances declined sharply in 6E after lake manipulation and did not recover subsequently, probably because of anoxia caused by decomposition of organic matter added to the water as a result of shoreline erosion. Weak correlations in regions 5 and 7 may have been an artifact of distance between the SIL weather station and region 5, and the development of an hypolimnetic oxygen deficit in region 7, if stratification occurred there due to impoundment.

Large fluctuations in abundances of natural populations occur commonly in response to a variety of natural phenomena, many of which cannot be predicted (Buchanan et al. 1978; Iker 1983; Bakun 1986). Many environmental monitoring studies operate on relatively short time frames and simply set out to record change, without giving much thought to the actual causes of those changes (Green 1984). Our research has demonstrated how easy it is to confuse natural variability with responses to anthropogenic perturbations, particularly when a response to weather predominates over a response to development. A combination of long-term basic monitoring, intensive surveys, and experimental studies allowed the error in interpretation of the monitoring data to be identified, and the mechanisms responsible for fluctuations in abundances of Hexagenia to be elucidated.

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Table 1. Correlation analyses between whole-lake Hexagenia abundance and air temperatures in Southern Indian Lake, 1972-1987. (See text for explanation; dd = degree days).

	Atmospheric dd>0°C for open-water season					
	Single year accumulations			Multi-year means		
	yr-1	yr-2	yr-3	1-yr	2-yr	3-yr
r^2	0.49	0.22	0.06	0.34	0.75	0.95
p	0.08	0.29	0.61	0.17	0.01	<0.001

Table 2. Average dates of break-up and freeze-up, length of ice-free season, and mean summer temperatures (°C) for Southern Indian Lake, 1972-1987.

Year	Break-up date	Freeze-up date	Ice-free days	Mean summer temperature (°C)
1972	25 May	20 October	148	11.4
1973	28 May	5 November	161	13.2
1974	7 June	20 October	135	11.4
1975	29 May	3 November	158	12.2
1976	26 May	3 November	161	13.5
1977	12 May	18 November	190	12.3
1978	31 May	13 October	135	10.8
1979	10 June	7 October	120	11.2
1980	10 May	9 October	151	11.3
1981	2 June	20 October	140	13.3
1982	1 June	19 October	141	11.7
1983	19 June	24 October	127	13.8
1984	5 June	22 October	139	13.7
1985	24 May	14 October	143	11.8
1986	31 May	10 October	133	11.4
1987	5 June	3 November	137	13.1

Table 3. Correlation analyses between air temperature accumulations [degree days) >0°C, open-water season] and water temperature accumulations dd>8°C) for regions 1, 2, 4, 5, and 6, Southern Indian Lake, 1972-1979.

	Region				
	1	2	4	5	6
r^2	0.71	0.68	0.58	0.68	0.72
p	0.02	0.02	0.05	0.02	0.02

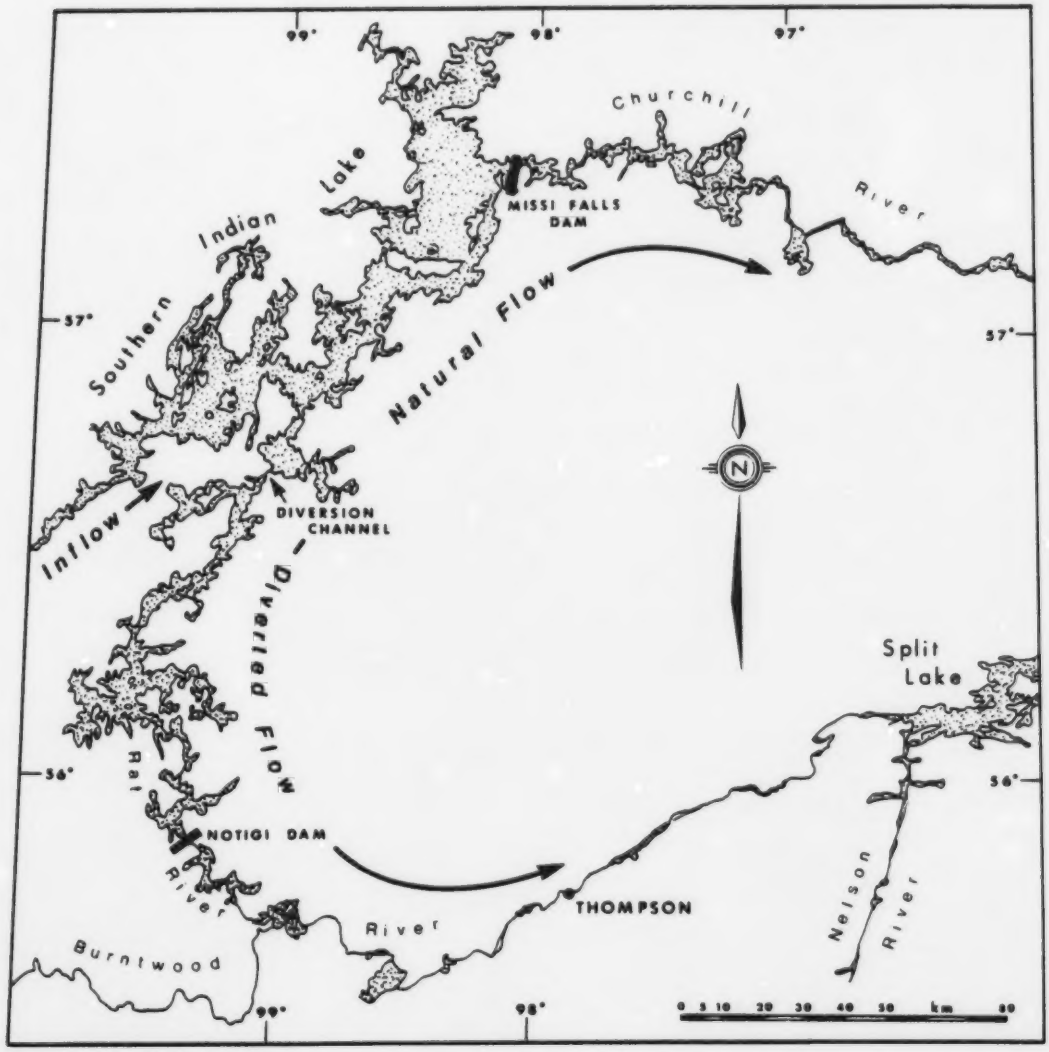

Fig. 1. Natural and diversion flows of the Churchill River in northern Manitoba (latitude in °N, longitude in °W).

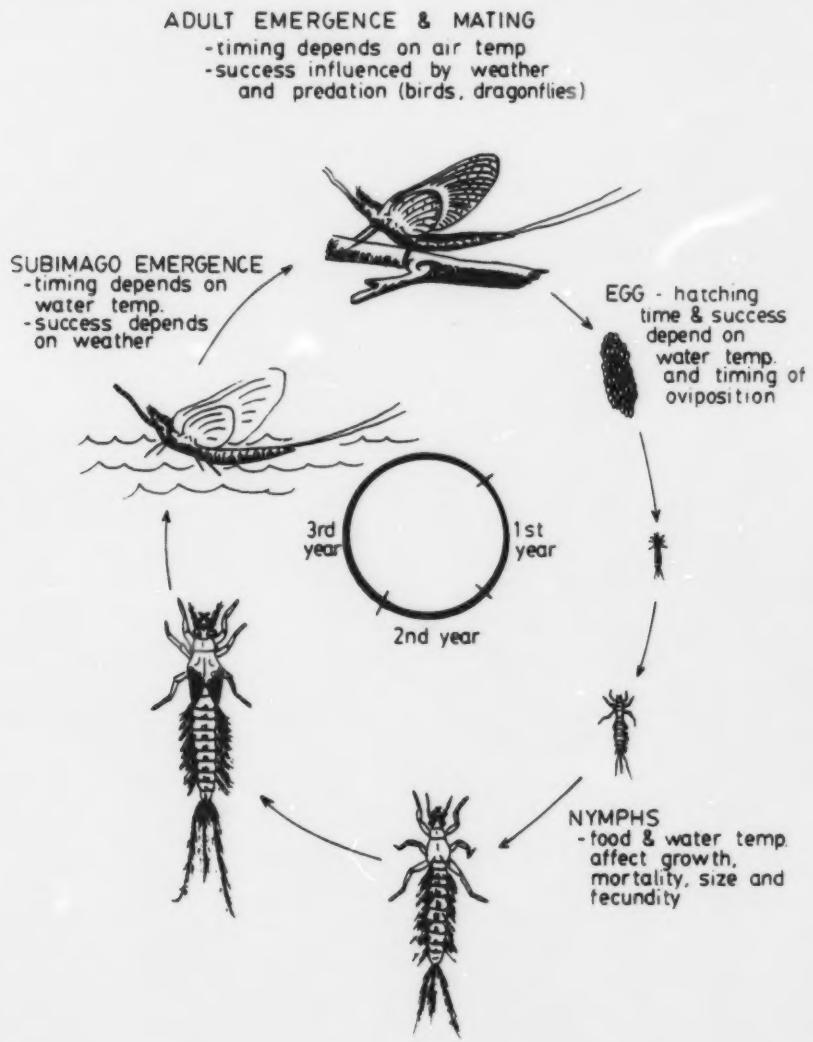
ADULT EMERGENCE & MATING
-timing depends on air temp
-success influenced by weather and predation (birds, dragonflies)
SUBIMAGO EMERGENCE
-timing depends on water temp.
-success depends on weather
EGG - hatching time & success depend on water temp. and timing of oviposition
3rd year
1st year
2nd year
NYMPHS
-food & water temp. affect growth, mortality, size and fecundity

Fig. 2. Summary of the 3-yr Hexagenia life cycle and the factors influencing abundance of Hexagenia in Southern Indian Lake (from Giberson 1991).

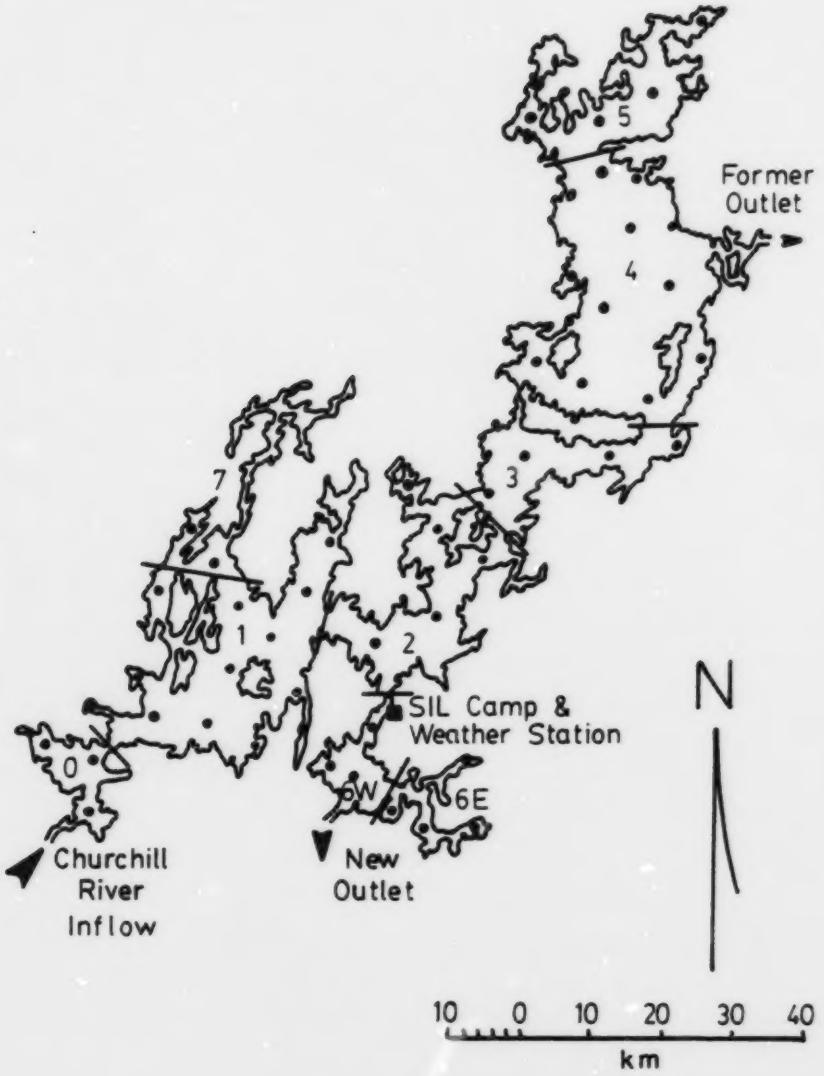

Fig. 3. Southern Indian Lake (SIL), showing regions (numbers), whole-lake survey sampling sites (dots), and location of the SIL camp and weather station. Arrows refer to major inflow and outlets.

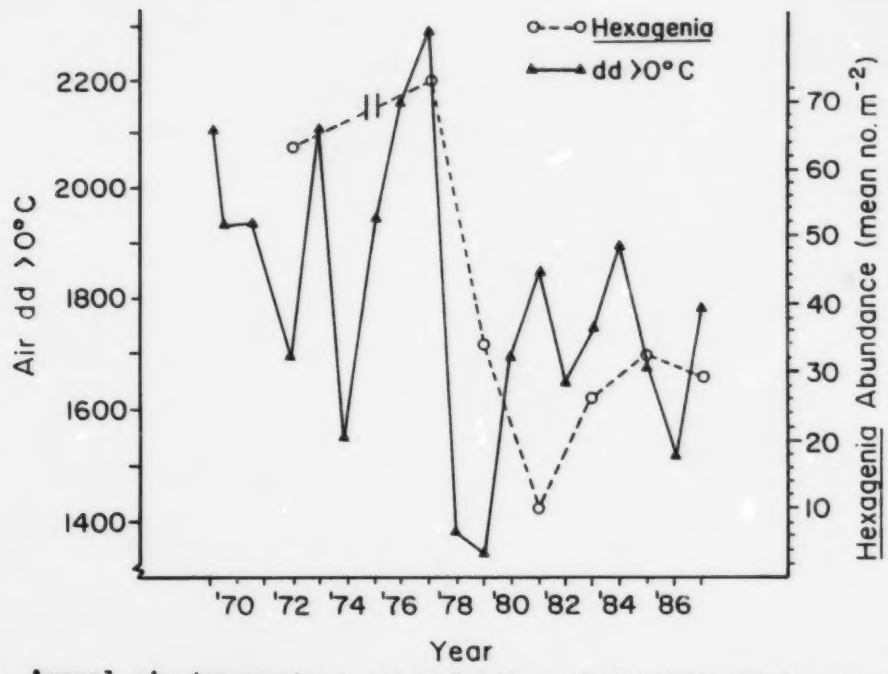

Fig. 4. Annual air temperature accumulations >0°C (1969-1987) and whole-lake Hexagenia abundance (no. m^{-2}, 1972-1987), for Southern Indian Lake (dd = degree days).

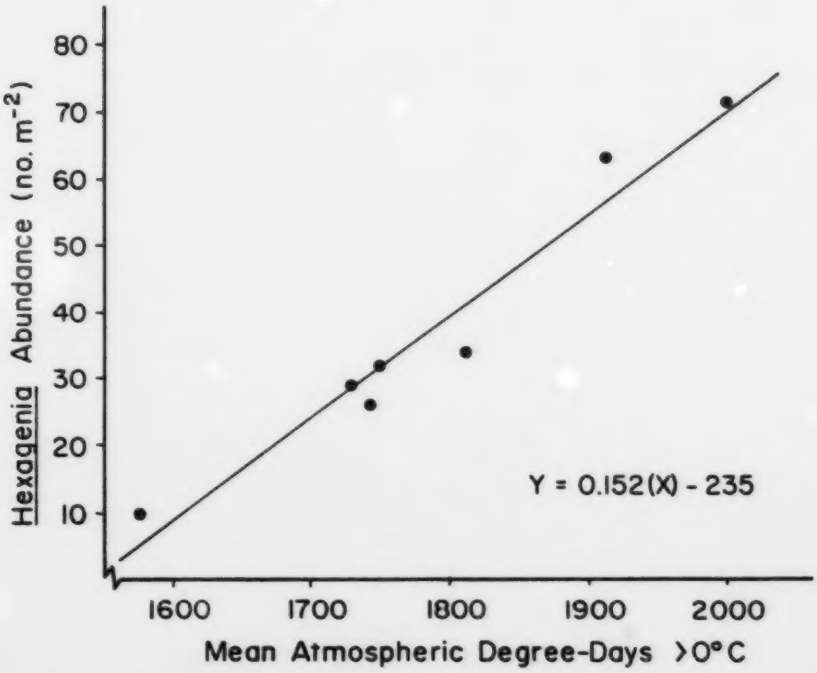

Fig. 5. Relationship between Hexagenia whole-lake abundance (mean no. m^{-2}) and 3-yr accumulated air temperatures (>0°C) in Southern Indian Lake, 1972-1987.

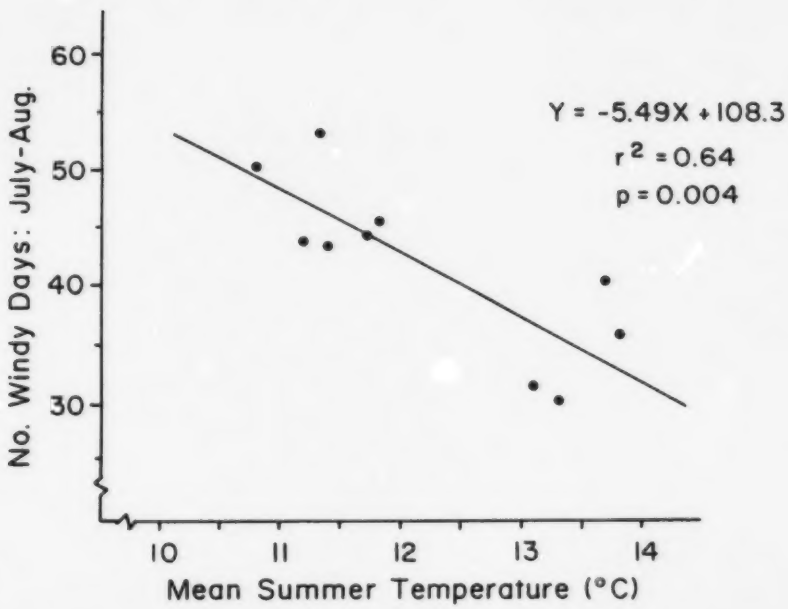

Fig. 6. Relationship between mean summer temperature (°C) and number of windy days during July and August for Southern Indian Lake, 1978-1989.

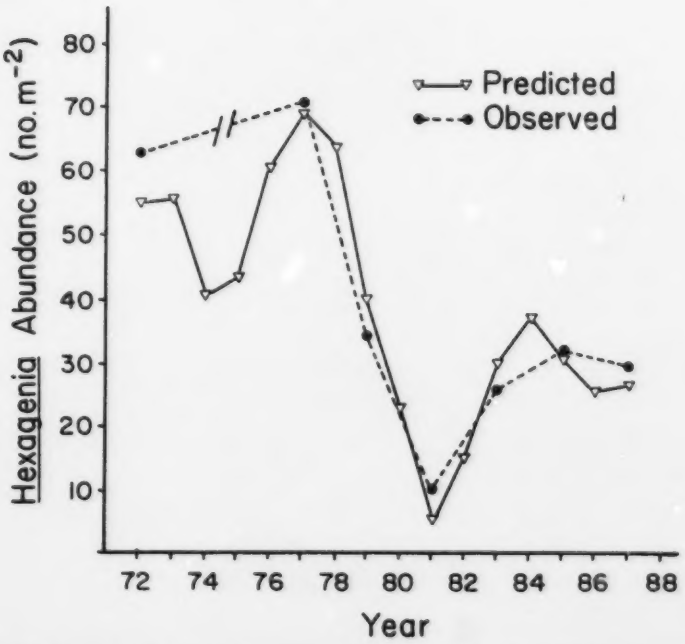

Fig. 7. Comparison between observed Hexagenia abundances and those predicted from the relationship shown in Fig. 5.

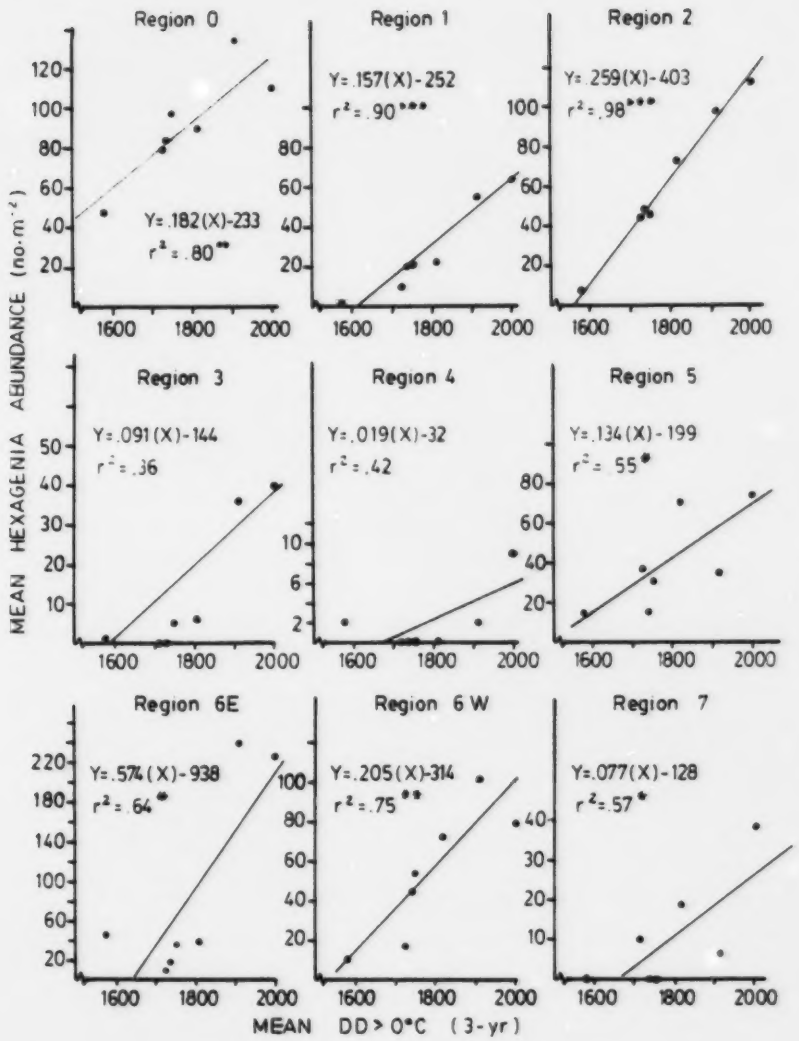

Fig. 8. Relationships between Hexagenia abundance and 3-yr accumulated air temperatures for the nine regions in Southern Indian Lake, 1972-1987. Asterisks refer to the level of statistical significance: *p<0.05; **p<0.01; ***p<0.001.

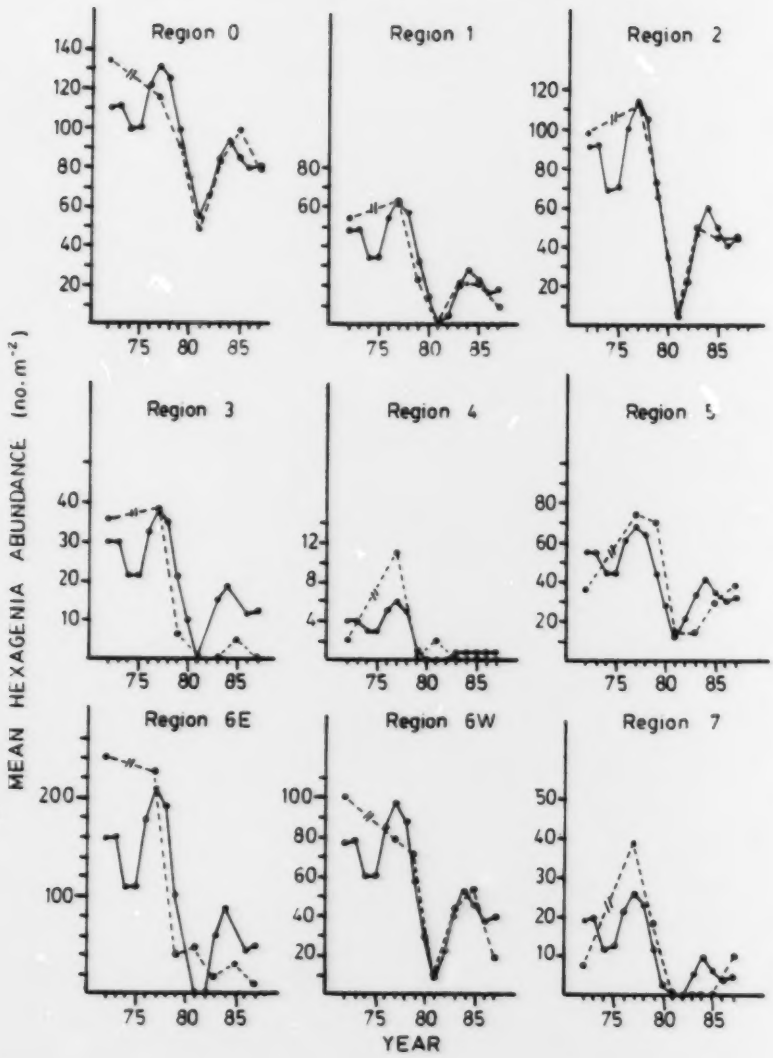

Fig. 9. Comparison between observed Hexagenia abundances (dashed line) and those predicted (solid line) from the relationships in Fig. 8.